A NEW ANGUIMORPH LIZARD FROM THE JURASSIC AND LOWER CRETACEOUS OF ENGLAND

by SUSAN E. EVANS

ABSTRACT. A new genus of anguimorph lizard *Parviraptor* (type species *P. estesi* sp. nov.) has been identified from middle Jurassic (Bathonian), and late Jurassic (Tithonian) or early Cretaceous (Berriasian) sites in England. The genus is also represented in the late Jurassic of Portugal (Oxfordian or Kimmeridgian, Guimarota). *Parviraptor* differs markedly from the only previously recorded Jurassic anguimorph, *Dorsetisaurus*, and shares a complex of characters which suggests that it was a stem-platynotan, and that the 'Platynota' had differentiated by the middle Jurassic.

THE published Jurassic record of crown-group lizards is drawn from a relatively small number of late Jurassic localities of which Solnhofen (Kimmeridgian, Germany), Guimarota (Oxfordian or Kimmeridgian, Portugal), and Como Bluff (Tithonian, North America) have been amongst the most productive (Estes 1983). Further important lizard material has come from the Purbeck Beds of Dorset, England. These beds were, until recently, considered to be of late Jurassic (Tithonian) age, and their vertebrate assemblage closely resembles that of Como Bluff. Allen and Wimbledon (1991), however, based on ostracode and palynomorph data, suggested that the Purbeck Limestone Formation may be of earliest Cretaceous (Berriasian) age. Representatives of at least three of the four currently recognized lizard subgroups – namely Gekkota, Scincomorpha and Anguimorpha, have been reported from Jurassic localities.

Jurassic anguimorphs have, until now, been represented by a single genus, *Dorsetisaurus*, known from Purbeck (Hoffstetter 1967), Como Bluff (Prothero and Estes 1980), and Portugal (the latter mistakenly under the name *Introrsisaurus*, Seiffert 1973). The supposed anguimorph *Lisboasaurus*, also from Portugal (Seiffert 1973), is a small theropod (Milner and Evans 1991), possibly a bird. Living anguimorphs are broadly divided into two groups – 'Anguioidea' (anguids, anniellids and xenosaurs, but the monophyly of this group is weakly substantiated (Estes *et al.* 1988)) and Varanoidea (*sensu* Pregill *et al.* 1986, varanids, lanthanotids and helodermatids). Varanoids form part of a larger group, 'Platynota' (*sensu* Pregill *et al.* 1986), which also encompasses a range of extinct genera including dolichosaurs, mosasaurs and their probable relatives – aigialosaurs. The taxonomic position of *Dorsetisaurus* in relation to the two main anguimorph lineages is uncertain, but previous workers (e.g. Hoffstetter 1967; Estes 1983; Borsuk-Bialynicka 1984) have placed it closer to anguioids. There is certainly nothing to suggest platynotan affinity and the earliest undisputed platynotans are currently the middle Cretaceous (Cenomanian–Turonian) aigialosaurs from Croatia (reviewed by Carroll and deBraga 1992). Kuhn (1958) described briefly a specimen from Solnhofen which he interpreted as a primitive platynotan, and named *Proaigialosaurus*. Unfortunately, the specimen was in an unnamed private collection and its present location is unknown. Hoffstetter (1964) suggested that *Proaigialosaurus* was a juvenile of the sphenodontian *Pleurosaurus*, but he had not examined the specimen. Kuhn's (1958) sketch represents the teeth as sharply pointed. If this is correct, then identity with *Pleurosaurus*, which has a typically sphenodontian dentition, is unlikely. Without the specimen, however, only speculation is possible.

Work on a middle Jurassic (Bathonian) microvertebrate assemblage from Kirtlington Cement

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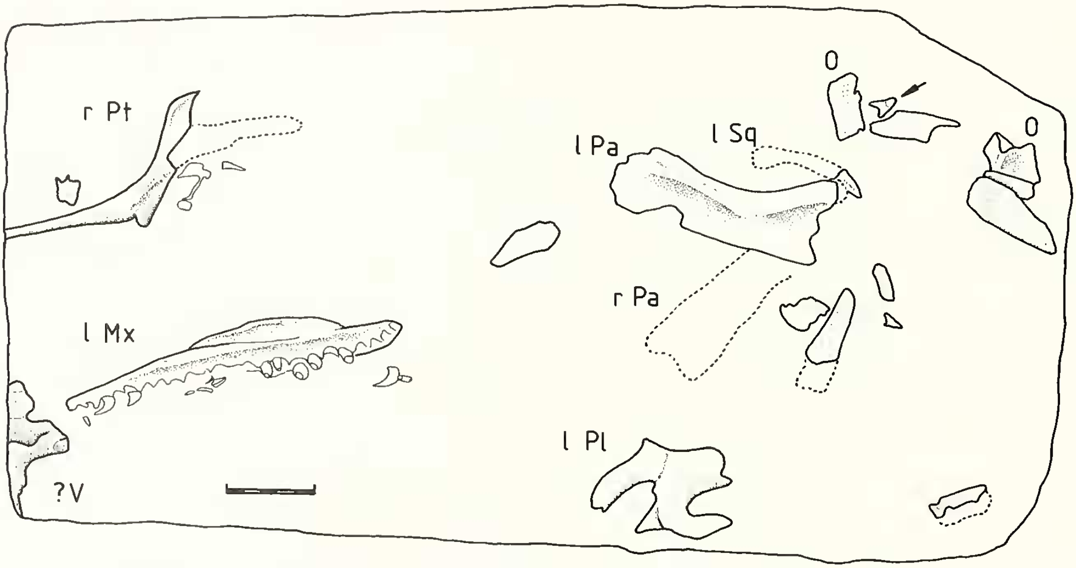
TEXT-FIG. 1. *Parviraptor estesi* gen. et sp. nov. BMNH 48388, holotype; Durlston Bay, Dorset; Purbeck Limestone Formation; × 2.



TEXT-FIG. 2. *Parviraptor estesi* gen. et sp. nov. BMNH 48388, holotype; Durlston Bay, Dorset; Purbeck Limestone Formation. Key: r, right; l, left; Mx, maxilla; O, osteoderm; Pa, parietal; Pl, palatine; Pt, pterygoid; Sq, squamosal; ?V, possible vertebral fragment. The arrow (top right) indicates the isolated archosaur tooth mentioned in the text. Scale bar represents 5 mm.

Works Quarry in Oxfordshire has yielded a new anguimorph which is strikingly different from *Dorsetisaurus* and shows characters suggestive of platynotan affinity. This new form is represented at Kirtlington by jaws, skull bones and vertebrae, associated on the basis of size, bone texture and, for the skull bones, complementary facets. Isolated bones of the same genus have subsequently been identified in material from Guimarota (Evans personal observations) but, until recently, there was no associated material. However, two partly associated specimens have recently been identified from Purbeck material in the collections of The Natural History Museum, London (BMNH). The first is a small block (BMNH 48388) found amongst undescribed material and bearing an association of skull bones, including a maxilla (Text-figs 1–2). The second (BMNH R8511) (Text-figs 3–4) was recovered from the pterosaur collection. The two specimens complement each other, and confirm the association of skull and vertebral elements suggested from Kirtlington. Since BMNH 48388 combines jaw and skull material, it is here designated as the holotype.

SYSTEMATIC PALAEONTOLOGY

SQUAMATA Oppel, 1911
ANGUIMORPHA Fürbringer, 1900
'PLATYNOTA' (*sensu* Pregill *et al.* 1986)
Genus PARVIRAPTOR gen. nov.

Derivation of name. From the Latin *parvus* meaning small, and *raptor* meaning robber.

Type species. Parviraptor estesi gen. et sp. nov.

Range. Middle Jurassic (Bathonian) to late Jurassic (Tithonian) or early Cretaceous (Berriasian) of England, with further material from the late Jurassic (Oxfordian or Kimmeridgian) of Portugal.

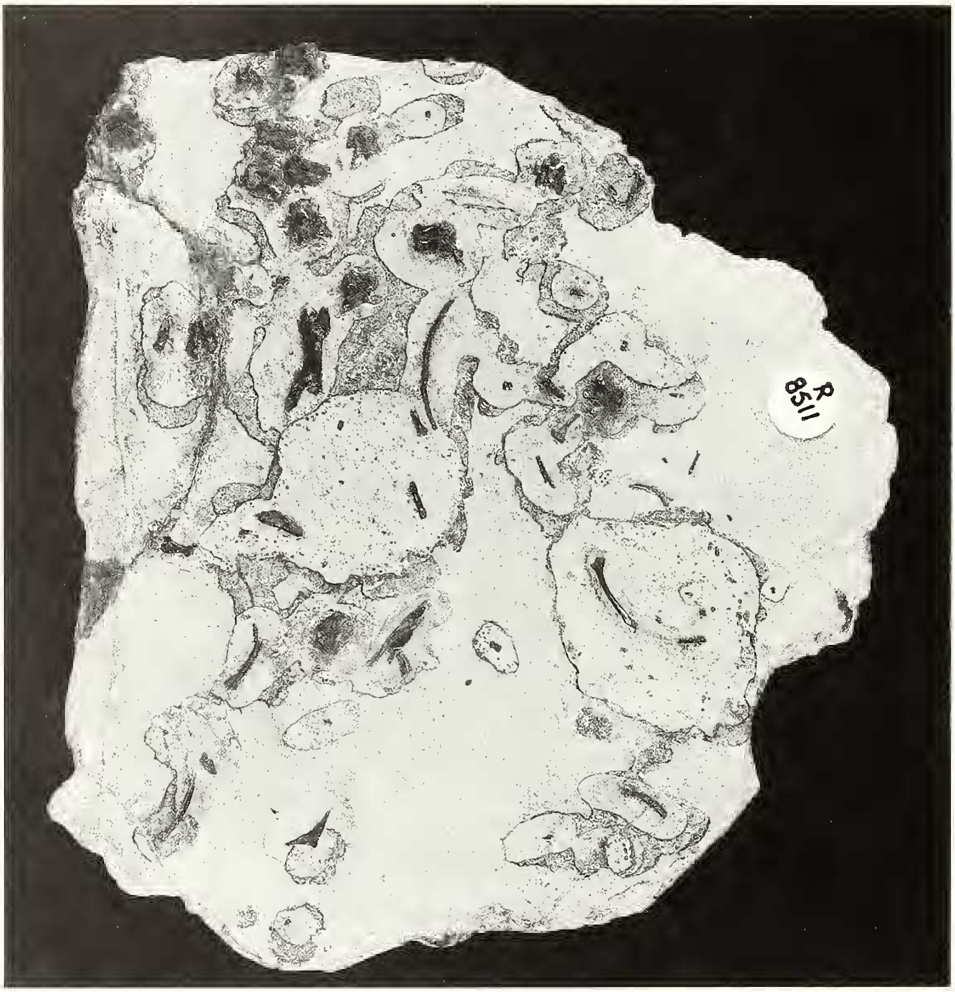
Diagnosis. A small (snout–vent length *c.* 150 mm) lizard characterized by a long, low maxilla, bearing at least twenty long, narrow and sharply recurved teeth with a circular cross-section; teeth pleurodont with shallow implantation, but each tooth position flanked by a build up of attachment bone; teeth attached to broad alveolar border; in lower jaw (not preserved on the holotype), deep lingual shelf present but subdental ridge lost, small intramandibular septum with fused lower edge; frontals and parietals paired; parietal foramen retained; well-developed subolfactory processes on frontals, meeting or nearly meeting in the midline; dorsal roofing bones without attached sculpture but compound sculptured osteoderms perhaps present on at least some parts of body; low maxillary facial process suggesting depressed antorbital region; elongated narial margin suggesting reduced contact between maxilla and nasal; palatine short and wide, narrow vomerine process, reduced pterygoid process; no palatine teeth and no choanal groove; prefrontal/palatine contact weak or ligamentous; pterygopalatine joint apparently weak; pterygoid long and slender, sharply incised by suborbital fenestra; narrow pterygoid flange with facet indicating ectopterygoid with an essentially anteroposterior orientation; pterygoids separated by large interpterygoid vacuity; presacral vertebrae procoelous, but notochordal canal closing late in development (at least in middle Jurassic form); accessory articulations present; axis intercentrum with hypapophysis, but no second hypapophysis on the rear of the axis centrum; cervical vertebrae short with deep prominent rib facets and well-developed spines; dorsal centra longer than cervicals; caudal vertebrae (Kirtlington) amphicoelous and autotomous.

Parviraptor estesi sp. nov.

Text-figures 1–4, 6A, C, 8A, 9, 10A, 13.

Derivation of name. For the late Dr Richard Estes, in recognition of his work on early lizards and their relationships.

Holotype. BMNH 48388, a small block bearing an association of skull bones. The specimen was originally part of the Beckles' collection. The block (Text-figs 1–2) bears parts of the skull of a small lizard including: the left parietal in ventral view (right in impression); a complete left maxilla in medial aspect; a right pterygoid in palatal aspect; a left palatine in dorsal aspect; and traces of the left squamosal. Other elements are too fragmentary for identification. There are isolated teeth and bone fragments near the pterygoid but it is not clear



TEXT-FIG. 3. *Parviraptor estesi* gen et sp. nov. BMNH R8511; Swanage, Dorset; Purbeck Limestone Formation; × 1.

whether these are of the upper or lower jaw. At one corner of the block is a fragment of what may be a vertebra; above it are two pustulate osteoscutes which probably, but not certainly, pertain to the lizard; one is keeled (Text-fig. 6c). Lying between them is an isolated, rooted, archosaur tooth (see below and Text-fig. 2, arrowed).

Type locality. Durlston Bay, Dorset (precise details unrecorded).

Type horizon: Purbeck Limestone Formation, late Jurassic (Tithonian) or early Cretaceous (Berriasian).

Diagnosis. As for genus, pending detailed comparisons between the specimens from the three localities.

Referred material. BMNH R8511, a small slab bearing an association of skull bones (right frontal, left parietal, left postfrontal or postorbitofrontal, left palatine), ribs and vertebrae (cervical and dorsal) recorded only as from the Middle Purbeck of Swanage, Dorset (Text-figs 3–4).

TEXT-FIG. 4. *Parviraptor estesi* gen. et sp. nov. BMNH R8551; Swanage, Dorset; Purbeck Limestone Formation. Key as for Text-figure 2, but in addition, At, atlas arch; Pf, postfrontal or postorbitofrontal; × 1.

Parviraptor cf. P. estesi

Text-figures 6B, 7, 8B–C, 11–12, 14–15.

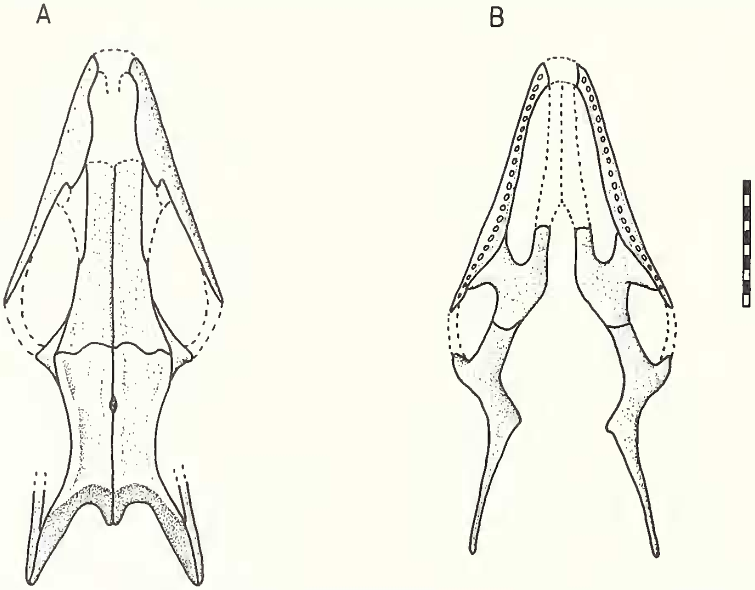
Material. A series of dissociated elements from the Mammal Bed horizon, Forest Marble (Bathonian), Kirtlington Cement Works Quarry, Oxfordshire, including: BMNH R12352, a partial left maxilla; R12353, a left parietal; R12354, a partial right dentary; R12355, the symphysial region of a right dentary; R12356, a partial left frontal; R12357, a left frontal of a juvenile; R12358, a left frontal of a juvenile; R12359, a partial left frontal; R12360, an axis vertebra; R12361, a partial dorsal vertebra; R12362, a partial dorsal vertebra; R12363, a dorsal vertebra of a juvenile; R12364, a fragment of a vertebral condyle; R12365, a dorsal vertebra; R12366, an anterior caudal vertebra; R12367, an anterior caudal vertebra; R12368, the anterior part of an autotomized caudal vertebra; R12369, the posterior part of an autotomized vertebra. A further collection of about 100 dissociated jaws, skull bones and vertebrae from the same horizon is held in the Department of Anatomy and Developmental Biology, University College London.

Comment. There is referable material (uncatalogued) from the late Jurassic (Oxfordian or Kimmeridgian) of Guimarota, Portugal, in the collections of the Freie Universität, Berlin.

Description. The description of *Parviraptor* is based on the Purbeck specimens in conjunction with referred material from Kirtlington Quarry, Oxfordshire.

Skull

The skull of *Parviraptor* is represented by the maxillae, parietals, frontals, a postfrontal or postorbitofrontal, pterygoids, palatines and dentaries, with a fragment of the squamosal (or possibly supratemporal). Recognition of these elements permits a partial reconstruction of the skull (Text-fig. 5A–B).

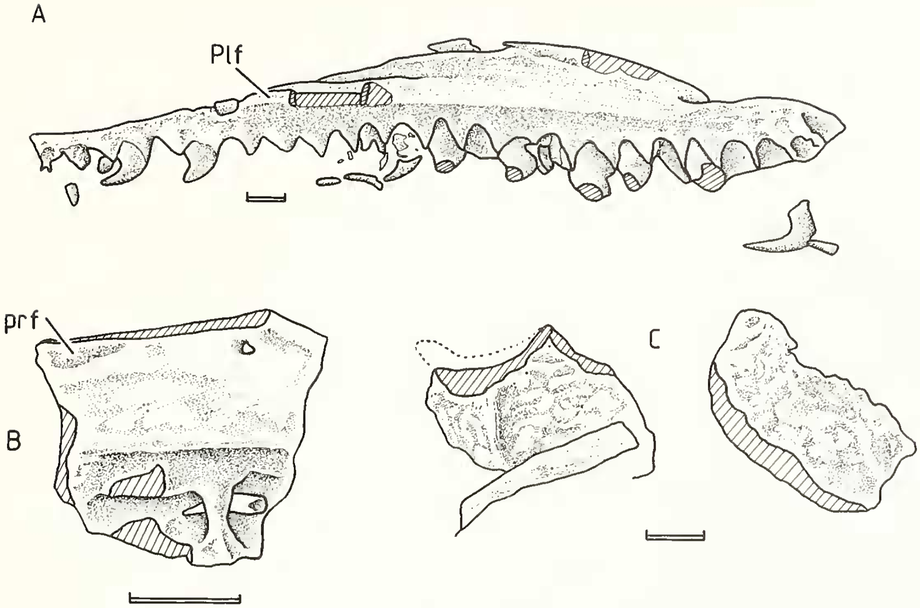


TEXT-FIG. 5. Partial reconstruction of the skull of *Parviraptor estesi* in A, dorsal, and B, palatal views. Scale bar represents 10 mm.

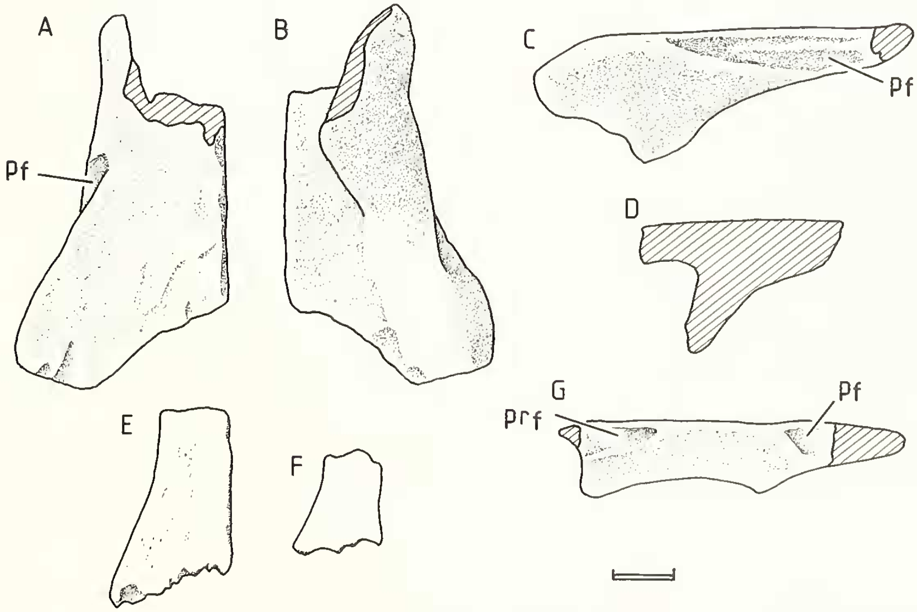
The maxilla has a long low facial process and shorter premaxillary and suborbital processes (Text-fig. 6A). The anterodorsal edge of the facial process is smooth and unbroken; it clearly formed an elongated narial margin in a depressed snout (as confirmed also by specimens from Guimarota). There is no obvious facet for the prefrontal but a narrow grooved region along the posterodorsal edge must have accommodated this element. The alveolar border bears around twenty-three tooth positions, most of which are filled. The implantation is pleurodont but there is a build-up of bone around each tooth base which provides a half socket. Most of the teeth are broken off near the base, but enough of the tips are preserved to show the distinctive shape. Each tooth has a round base and a long, sharp, recurved tip – quite different from the broader, almost triangular teeth of *Dorsetisaurus*. Only one tooth shows a trace of a replacement pit in the form of a scarred area on the distolingual surface. This feature, and the occasional presence of a similar excavation in the bone of attachment suggests an essentially anguimorph mode of replacement. The palatal shelf of the maxilla is relatively broad, but the lingual edge is smooth and clearly did not meet the vomer (the palaeochoanate condition). The position of the palatine facet is marked by a weak groove about half-way along the bone – the edge immediately behind this being broken. However, the length of the facet matches that of the corresponding process from the palatine, suggesting that the maxilla extended for a short distance into the margin of the suborbital fenestra. The entry foramen for the maxillary nerve lies close to the facet.

The Kirtlington maxillae are fragmentary and add little to the holotype description. On the medial surface, however, some specimens show what appears to be a prefrontal facet. This feature is larger than anything preserved on the holotype maxilla but, by comparison with Portuguese material, the difference is probably due to damage. R12352 (Text-fig. 6B) is a maxillary fragment which preserves a displaced replacement tooth. This tooth is similar to those of the holotype and is matched by isolated teeth from the fine sievings.

There is no frontal bone on the holotype block, but BMNH R8511 from Purbeck preserves a right frontal

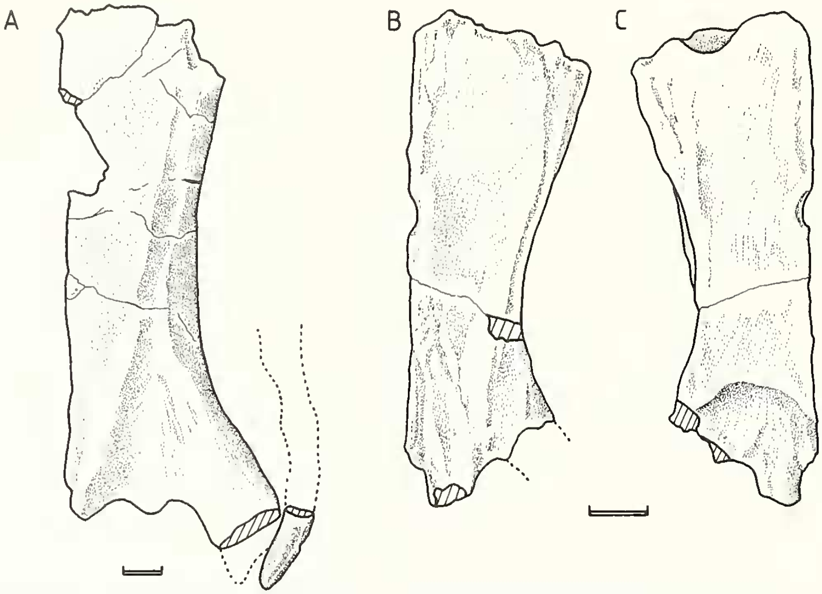


TEXT-FIG. 6. *Parviraptor estesi* gen. et sp. nov. A, BMNH 48388, holotype maxilla; lingual view. B, BMNH R12352; maxillary fragment from Kirtlington. C, BMNH 48388; compound osteoscutes on holotype block. Scale bars represent 1 mm.



TEXT-FIG. 7. *Parviraptor* cf. *P. estesi*. Kirtlington; Forest Marble, (Bathonian). A–D, BMNH R12356; posterior region of left frontal in A, dorsal, B, ventral, and C, lateral views. D, cross-section, to show development of subolfactory process. E, BMNH R12357; and F, BMNH R12358; same region in juveniles for comparison of size. G, BMNH R12359; lateral view of left frontal to show facets for circumorbital bones. Scale bar represents 1 mm.

in lateral view (Text-fig. 9B) showing the facets for the pre- and postfrontal (or postorbitofrontal) and the deep subolfactory process which stretches toward the midline. Lying against the rear of the subolfactory process is a second element which appears to be either weakly ossified or simply calcified and is most reasonably interpreted as the orbitosphenoid. Similar frontals are known from Kirtlington (Text-fig. 7). They vary in size and are always paired with a simple straight midline suture and little orbital waisting. The dorsal surface is flat, matt and completely unsculptured. The posterior border is 'U'-shaped, but the frontoparietal joint appears to have been weak. The subolfactory processes are strongly developed (Text-fig. 7D), but incomplete. The posterior facet for the postorbitofrontal, or postfrontal, is large, but shallow and mostly ventral. As a result, the articulation between the postorbitofrontal and frontal is unlikely to have limited mesokinesis.

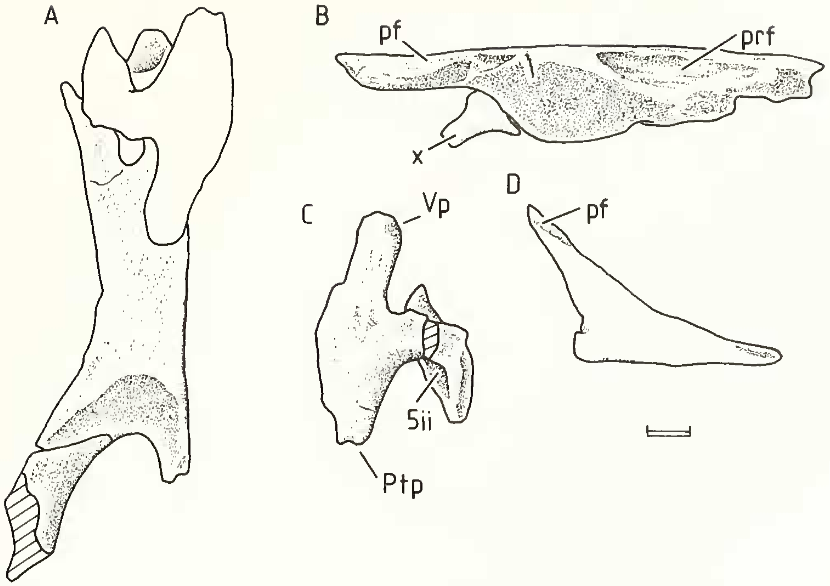


TEXT-FIG. 8. *Parviraptor estesi* gen. et sp. nov. A, BMNH 48388, holotype; left parietal and associated squamosal; ventral view. B–C, BMNH R12353; left parietal from Kirtlington in B, ventral and C, dorsal views. Scale bars represent 1 mm.

The parietals (Text-figs 7A, 8A) on the Purbeck blocks are large paired bones with a small parietal foramen. Each bone is longer than it is broad, and the two parietals together formed a substantial plate (Text-fig. 5A). The lateral margins are curved and clearly bordered a long upper temporal opening. Running along the ventrolateral edge is a conspicuous groove, presumably for the *taenia marginalis* of the chondrocranium. There are no descending flanges and the jaw adductor muscles do not appear to have been strongly developed; presumably with the sharp recurved teeth, a quick snapping bite was enough to subdue prey before swallowing. Posteriorly, each bone tapers laterally into a strong postparietal process and medially into a smaller triangular process which extended out over the supraoccipital and may have been in contact with it. As preserved, the postparietal processes bear no obvious facets and the supratemporal or squamosal must have attached further distally. Anteriorly, the two parietals contribute towards a broad median frontal process while laterally there is a small, but conspicuous, notch for the posterolateral part of the frontal. In dorsal view (Text-figs 8C, 9A), the surface is smooth but bears a strong posterior surface for the attachment of cervical muscles.

The largest Kirtlington parietal (R12353; Text-fig. 8B–C) is complete except for its postparietal process, and is almost identical to that on BMNH 48388 except that it is proportionally a little shorter. The anterior border is slightly wider than the posterior one and bears a small shelf facet for the frontal. There is no obvious facet for the postorbitofrontal, but it probably fitted below the overhanging dorsal rim of the parietal – as it does in *Varanus*.

At one end of BMNH R8511, there is a slender triradiate bone with long anterior and posterior rami and a short blunt external process (Text-fig. 8D). In its general shape and size, this element could be taken for a jugal but it lacks a smooth orbital margin and the distribution of facets is incompatible with such an interpretation. The bone is more plausibly interpreted as a postfrontal, or postorbitofrontal, and can be fitted



TEXT-FIG. 9. *Parviraptor estesi* gen. et sp. nov. Skull bones from BMNH R8511. A, left parietal with overlying palatine in outline; B, right frontal in lateral view. C, left palatine in ventral view. D, probable left postfrontal (or postorbitofrontal) in dorsolateral view. Key: pf, postfrontal facet or (D) region of postfrontal which fits into this facet; prf, prefrontal facet; Ptp, pterygoid process; Vp, vomerine process; x, possible orbitosphenoid; 5ii, canal for maxillary nerve. Scale bar represents 1 mm.

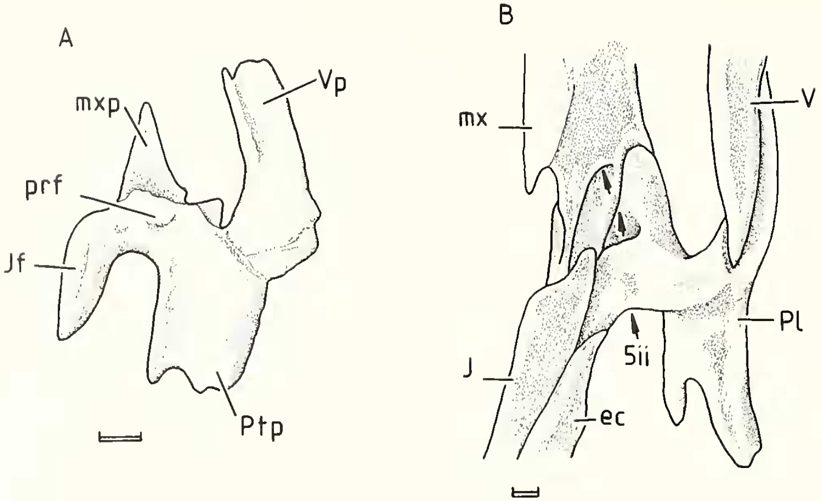
against the frontoparietal suture. The faceted anterior ramus thus fits into the facet on the frontal while the apparently unfaceted posterior ramus presumably had a weaker articulation with the parietal (see above). The bone is embedded in matrix and its undersurface is not visible. It is unclear how, or even whether, this element articulated with other circumorbital or temporal bones.

Lying beside the left parietal of the holotype block, partly in impression, is a slender squamosal (Text-fig. 8A). This lacks a dorsal process and is typically scleroglossan.

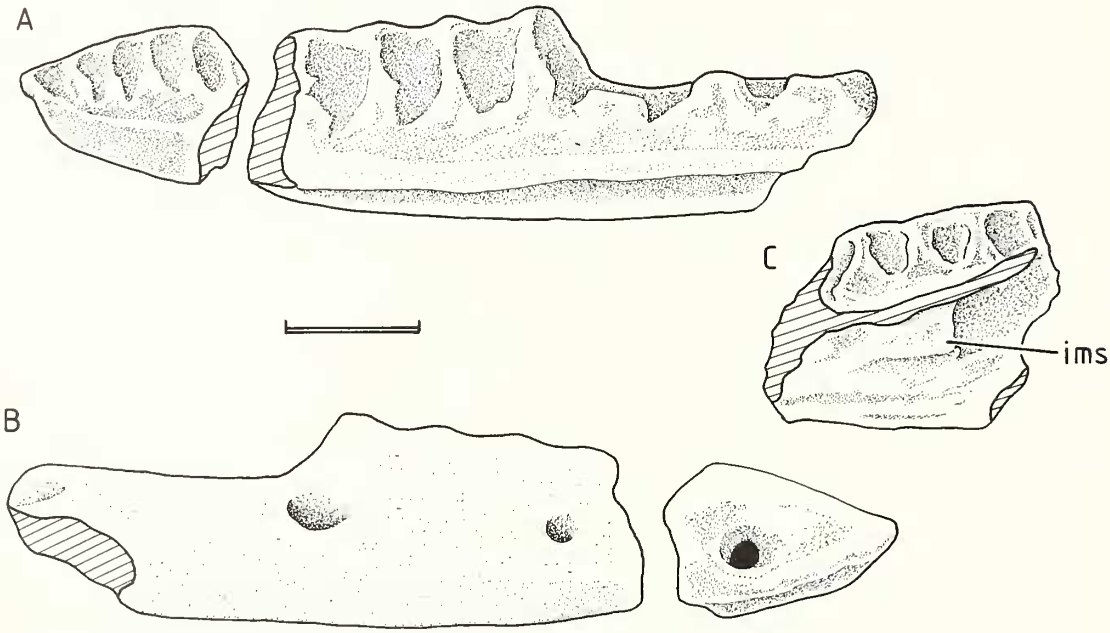
The left palatine is preserved in dorsal view (Text-fig. 10A) on the holotype and in ventral, palatal, view on BMNH R8511 (Text-fig. 9C). It is triradiate and roughly as wide as it is long. The slender vomerine process has a notched anterior border and a long choanal margin. By contrast, the posterior process is short and clearly had a weak transverse joint with the pterygoid which may have permitted hypokinetic palatal hinging (Frazzetta 1962). The lateral maxillary process has splayed anterior and posterior limbs. The posterior limb is slightly raised and bears a groove facet for the anteromedial part of the jugal. It is pierced by a short canal for the maxillary nerve (Text-fig. 9C). The neck of the palatine, between the maxillary process and palatal plate, bears a slight rugosity for the prefrontal but this is not prominent (prf. Text-fig. 10A) and the contact may have been ligamentous. There is no trace of palatine teeth, nor is there a choanal groove or gutter. From the shape of the palatine, both the choana and the suborbital fenestra were narrow. In its structure and relations, the palatine of *Parviraptor* is much like that of a modern *Varanus* (Text-fig. 10B).

The right pterygoid is preserved in palatal view (Text-fig. 2). It shows a long, tapering quadrate process and a slender, forked palatal plate. At the medial junction of the two, the recess for the basipterygoid process of the sphenoid is flanked by a conspicuous knob. Laterally, the pterygoid flange is slightly hook-shaped with a distinct ectopterygoid facet. The two bones clearly slotted into one another with the ectopterygoid orientated essentially anteroposteriorly rather than mediolaterally.

The dentary is known only from Kirtlington. The largest dentary fragment is BMNH R12354 (Text-fig. 11A–B), the midportion of a right bone. The lateral surface is pierced by large, widely spaced sensory foramina. Medially, the bone has a deep, almost vertical, alveolar shelf with no development of a subdental ridge. The tooth positions are marked by walls of alveolar bone which clearly built up around the bases of the teeth, although they do not appear to have held the teeth in place because all specimens are edentulous. The Meckelian fossa is very shallow and opens ventromedially. As preserved, there is no obvious splenial facet. In



TEXT-FIG. 10. A, BMNH 48388; left palatine of *Parviraptor estesi* on holotype block, dorsal view. B, left palatine and associated bones of *Varanus* sp. Key: ec, ectopterygoid; J, jugal; Jf, jugal facet; mx, maxilla; mxp, maxillary process; Pl, palatine; prf, prefrontal boss; Ptp, pterygoid process; V, vomer; Vp, vomerine process; 5ii, course of maxillary nerve. Scale bars represent 1 mm.



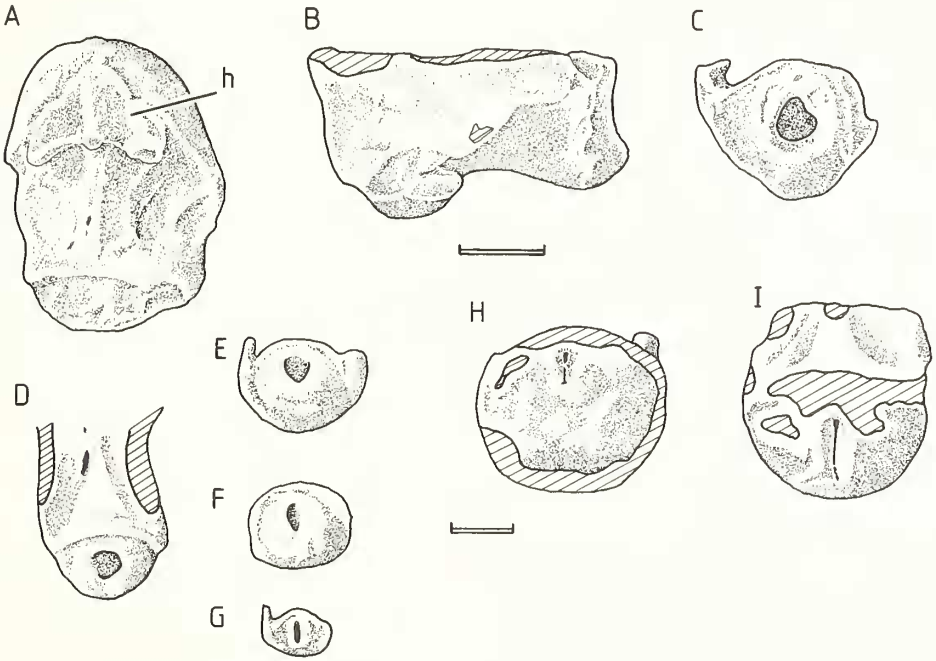
TEXT-FIG. 11. *Parviraptor* cf. *P. estesi*; Kirtlington; Forest Marble, (Bathonian). A–B, composite right dentary comprising BMNH R12355, symphysial region, and BMNH R12354, midsection. A, lingual, and B, labial views. C, BMNH R12370 posterior fragment in lingual view to show intramandibular septum (ims). Scale bar represents 1 mm.

Text-figure 11, an isolated symphysial region (R12355) has been included. The symphysis bears a dorsomedial flange which met the opposite bone in the midline. Ventrolaterally, there is a single large sensory foramen. The rear end of the tooth row is preserved in BMNH R12370. Beneath the alveolar border, there is a small intramandibular septum, separating the entry of the inferior alveolar canal from the Meckelian fossa itself (Text-fig. 11c).

The postcranial skeleton

Vertebrae. Of the lizard vertebrae at Kirtlington, only one set matches the jaw and skull material in terms of size and surface texture, and this association is confirmed by BMNH R8511 from Purbeck.

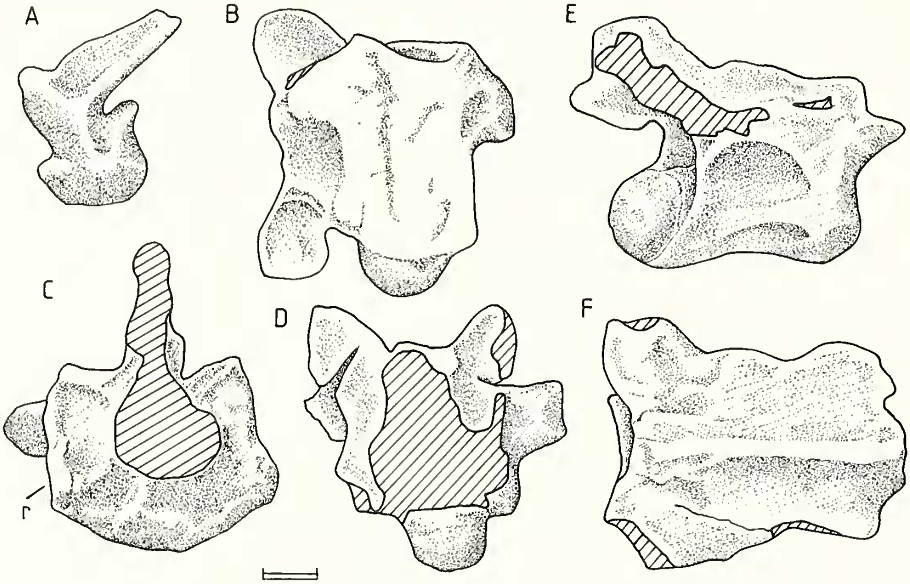
The vertebrae in question are among the most numerous of the lizard vertebrae at Kirtlington and, like the frontals and parietals, show a considerable size range. They also show what appears to be an interesting ontogenetic series which correlates with size and illustrates the development of the posterior condyle (Text-fig. 12D–I). In general, the vertebrae are strongly built, with a large anterior cotyle pierced centrally by a notochordal canal. The dorsal surface of the centrum bears a conspicuous ridge. The very smallest centra are free of the neural arches, but small fused vertebrae are fully notochordal (e.g. Text-fig. 12G). In slightly larger specimens, a lip of bone appears on the posteroventral edge of the centrum (e.g. Text-fig. 12D–E). This increases in size, spreading upward to form a grooved process. When fully developed, the sides of the grooves have met in the midline leaving a condyle with a small hole or pit to mark the original position of the notochord (Text-fig. 12H–I). This is the development process followed in the development of lizard procoely (Winchester and Bellairs 1977), but it is unusual to find all stages within a series of posthatchling vertebrae (except in procoelous geckos and xantusiids). Even when the condyle is fully formed, the notochordal canal remains open within the remainder of the vertebra.



TEXT-FIG. 12. *Parviraptor* cf. *P. estesi*. Kirtlington; Forest Marble, Bathonian. A–C, BMNH R12360; axis centrum, in ventral, left lateral, and posterior views (Key: h, hypapophysis). D–M, range of dorsal vertebrae to show size-related stages in the development of the posterior condyle. D–E, BMNH R12361, dorsal and posterior views; F, BMNH R12362, posterior view; G, R12363; posterior view. H–I, BMNH R12364; posterior and dorsal views. Scale bars represent 1 mm.

This apparent ontogenetic series is interesting. Each of the other lizards at Kirtlington shows a notable uniformity of size in its individual elements, as would be expected in a group normally characterized by determinate growth. This is clearly not true of *Parviraptor* where the vertebrae, as well as the frontals and parietals, despite a constant morphology, show a range of sizes which may indicate a relatively long period of growth before reaching adult size. It raises the question as to whether any of the Kirtlington specimens are actually adult. The largest Kirtlington parietals are only about half the size of those on the holotype block, while some of the Guimarota bones are two or three times the size of comparable Purbeck elements. Furthermore, the vertebrae on BMNH R8511, although of similar size to those from Kirtlington, have fully developed condyles with no trace of the notochordal canal. Whether these variants represent several different-sized species or a series of developmental stages within a single species is impossible to determine at the present time.

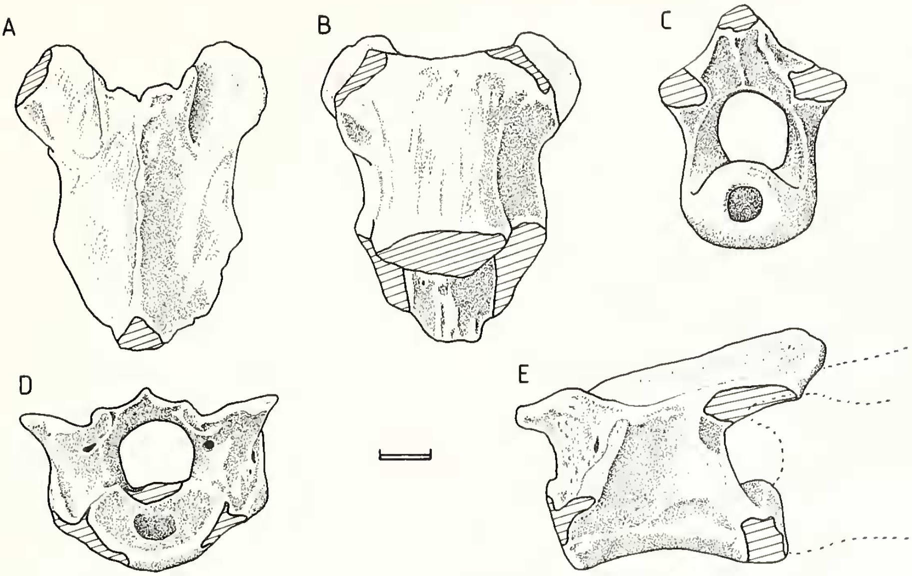
On the basis of specimens from both Kirtlington and Purbeck, representative elements from most regions of the vertebral column have been identified. An isolated atlas arch is preserved on BMNH R8511 (Text-fig. 14A), but the only known axis vertebrae are those from Kirtlington. The axis (Text-fig. 12A–C) bears a small odontoid process and there is a prominent hypapophysis on the intercentrum. The posterior end of the centrum is notochordal, but there is some development of the ventral lip. There is, however, no trace of a second, posteriorly placed, hypapophysis.



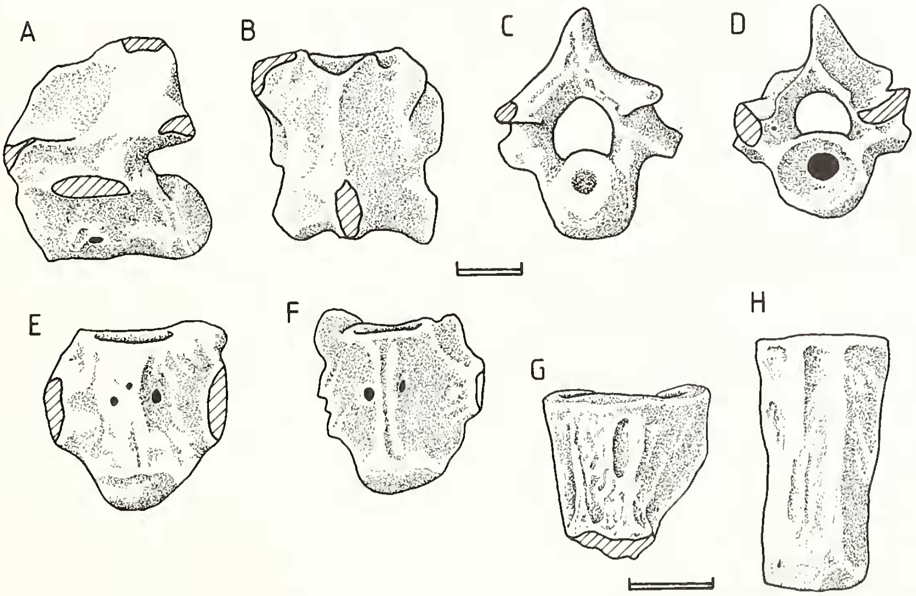
TEXT-FIG. 13. *Parviraptor estesi*. BMNH R8511; Swanage, Dorset; vertebrae. A, right atlas arch in lateral view. B, cervical vertebra in left ventrolateral view. C, fragmentary cervical vertebra in end view to show deep rib facets and neural spine. D, cervical vertebra in dorsal view. E, dorsal vertebra in right lateral view. F, dorsal vertebra, dorsal view. Key: r, rib process. Scale bar represents 1 mm.

Cervical vertebrae are preserved on BMNH R8511. They are shorter than the dorsals and bear deep, prominent rib facets (Text-fig. 13B–D) and well-developed neural spines. Unfortunately, none is sufficiently well preserved in ventral view to determine the presence or position of cervical hypapophyses. Dorsal vertebrae are known from both Kirtlington and Purbeck (Text-figs 13E–F, 14). The centrum is broad, almost rectangular (Text-fig. 14B), and lacks subcentral foramina. The neural arch is wide and bears large, flared anterior and posterior zygapophyses with a rudimentary zygosphene/zygantrum system (Text-fig. 14A, D), but there seems to be little development of the neural spine.

Caudal vertebrae are known only from Kirtlington. Anterior caudal vertebrae bear transverse processes and typical neural spines (Text-fig. 15A–F). The midventral groove becomes rugose and pitted as the region of autotomy is approached. The presence of several hemivertebrae showing the characteristic midline transverse



TEXT-FIG. 14. *Parviraptor* cf. *P. estesi*. BMNH R12365; Kirtlington; Forest Marble, (Bathonian). Dorsal vertebra, in dorsal, ventral, posterior, anterior, and left lateral views. Dotted lines in E show overlap between successive vertebrae. Scale bar represents 1 mm.



TEXT-FIG. 15. *Parviraptor* cf. *P. estesi*. Kirtlington; Forest Marble, (Bathonian). A–E, BMNH R12366; anterior caudal vertebra; in left lateral, dorsal, posterior, anterior, and ventral views. F, BMNH R12367; anterior caudal in ventral view, showing groove for caudal blood vessels. G–H, fragments of autotomous vertebra G, BMNH R12368; short portion anterior to fracture plane; H, BMNH R12369; longer portion posterior to fracture plane (cranial end uppermost in each case). Scale bars represent 1 mm.

ridge confirms that the tail contained functional autotomy planes. There were apparently no transverse processes on autotomous vertebrae but the fracture plane divided the vertebra into a small anterior component and a longer posterior one (Text-fig. 15G–H). The absence of any complete middle or posterior caudals suggests that most elements of the tail retained autotomy septa. The caudal vertebrae share the thick central lips of the presacrals, but remain notochordal.

Ribs. A set of strong single-headed ribs is preserved on BMNH R8511 (Text-figs 3–4).

Discussion. The fully pleurodont dentition, the simple arched squamosal and the appearance of a mesokinetic hinge line in the palate and skull roof suggest that *Parviraptor* was a crown-group lizard. This conclusion is further supported by the relatively short jaws (primitive relatives typically have long narrow jaws; Evans 1980, 1991) and procoelous vertebrae.

Determining the position of *Parviraptor* within lizards is more complicated, since (following Estes 1983; Estes *et al.* 1988) it appears to show a combination of gekkotan and anguimorph character states. Kluge's detailed analyses of modern gekkotans (e.g. 1967, 1987) have suggested that paired parietals and the posthatchling retention of a notochordal canal are synapomorphies of Gekkota, resulting from paedomorphosis. Consequently, fossil lizards exhibiting one or other of these character states have frequently been classified as gekkotans (Estes 1983). However, some of the same character states (paired parietals, free trunk intercentra, centrum development) are also present in living xantusiids, once classified with Gekkota but now generally regarded as scincomorphs (Estes *et al.* 1988), and some specimens of *Varanus* retain a midline suture in the anterior part of the parietal (personal observations). Clearly then, the same states have arisen more than once within crown-group lizards. The retention of paired parietals in *Parviraptor*, and the late formation of the vertebral condyle, are just as likely to be the result of its extended growth period as an indication of gekkotan relationship.

Taking this into account, the majority of the derived characters displayed by *Parviraptor* suggest anguimorph, rather than gekkotan, affinity (Borsuk-Bialynicka 1984; Pregill *et al.* 1986; Estes *et al.* 1988):

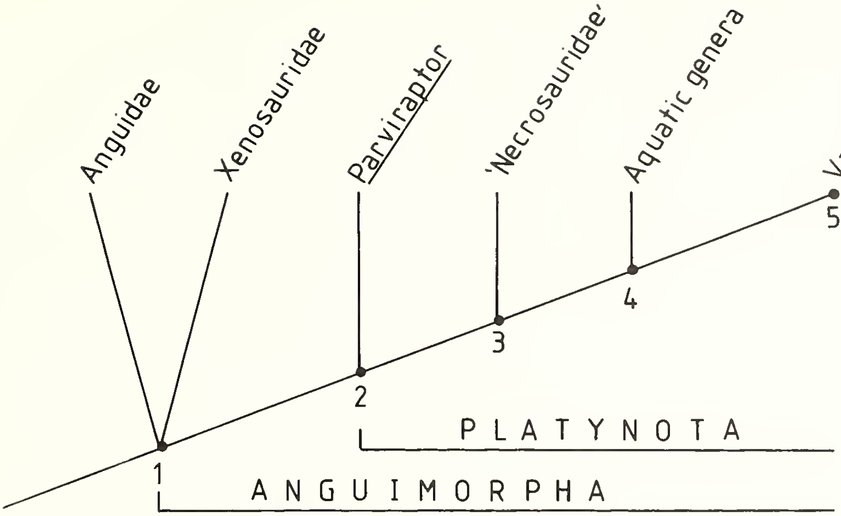
(a) intramandibular septum (although a small septum can be present in iguanians and lacertoids)
(b) shallow pleurodont implantation with bone of attachment; replacement pits lost or reduced – tooth replacement may be distolingual
(c) deep lingual shelf but no subdental ridge
(d) Meckel's canal opens anteroventrally
(e) probably compound osteoscutes (although these are found in a few other groups).

There is, however, a problem. In all living anguimorphs, cervical hypapophyses attach to the rear of the preceding centrum. They are fused to the centrum in anguids and sutured to it in varanoids. The preservation of this region of the column in *Parviraptor* is admittedly poor, but it is disturbing that no trace of hypapophyses, nor of a sutural surface for a hypapophysis, is visible behind the level of the atlas intercentrum.

Within Anguimorpha, *Parviraptor* is strikingly different from *Dorsetisaurus* in its sharp recurved teeth, the low maxilla, the presence of an intramandibular septum, the absence of dermal sculpture on the roofing bones, the structure of the vertebrae, the shape of the parietals and the apparently extended growth period.

Comparison with both living and extinct anguimorph genera, using principally the character sets of Borsuk-Bialynicka (1984), Pregill *et al.* (1986) and Estes *et al.* (1988), produces conflicting hypotheses. In a number of features, *Parviraptor* resembles platynotan lizards:

(a) the absence of osteodermal incrustation on the skull bones (osteoderms and dermal ornament are usually free of the skull bones in platynotans. *Heloderma* may be specialized in this respect; it has a tesselate arrangement of cranial osteoderms which become attached to the underlying bones)



TEXT-FIG. 16. Cladogram showing hypothetical relationships for *Parviraptor* based on the work of Estes (1983), Borsuk-Bialynicka (1984) and Pregill *et al.* (1986). Key: Node 1, Anguimorpha (intramandibular septum; replacement teeth usually posterolingual; loss/reduction of subdental ridge; Meckel's groove opens anteroventrally; dorsal and cephalic osteoderms); Node 2, Platynota (*sensu* Pregill *et al.* 1986) (well-developed subolfactory processes on frontals; teeth unicuspid, recurved, trenchant; reduction in maxillary/nasal contact; vomers narrow, more than twice palatine length; palatine as wide as it is long; osteoderms free of skull bones); Node 3, unnamed taxon (parietals fused; adductor muscles extend onto dorsal surface of parietal; splenial/dentary overlap reduced; vertebral condyle oblique [?R in aquatic genera] and waisted; postaxial cervical centra with fused hypapophyses bearing separate epiphyses); Node 4, unnamed taxon – aquatic genera denote aigialosaurs and mosasaurs (retracted nares; frontal trapezoid; maxilla does not underlie orbit; facial process of maxilla set posteriorly; plicidentine present [varies in 'necrosaurs']; reduced overlap of dentary and postdentary bones; separate epiphyses on cervical hypapophyses [varies in 'necrosaurs']; loss of caudal autotomy); Node 5, Varanoidea (*sensu* Pregill *et al.* 1986, i.e. Varanidae, Lanthanotidae, Helodermatidae) (subolfactory processes of frontals usually meet in the midline; fewer than 13 maxillary teeth; supratemporal extends anterior to level of parietal notch).

(b) a palatine that is as wide as it is long, has no choanal groove, lacks denticles, and has a weak prefrontal boss suggestive of a ligamentous attachment between the palatine and prefrontal
(c) the long slender vomers (as deduced from the reconstruction – but since the length of the maxilla, the position of its facet with the palatine, and the shape of the palatine are all known, this is not speculative)
(d) the wide interpterygoid vacuity
(e) the sharp, unicuspid, strongly recurved teeth
(f) the depressed form of the maxilla with its elongated narial margin
(g) the strongly developed subolfactory processes.

There are, however, character conflicts and *Parviraptor* lacks a number of character states found in living varanoids (Pregill *et al.* 1986; Estes *et al.* 1988) notably:

(a) the presence of plicidentine (infolding at the tooth base)
(b) the invasion of the dorsal surface of the parietal adductor musculature
(c) the presence of sutural surfaces at the rear of each cervical vertebra for the attachment of hypapophyses
(d) the anterior elongation of the supratemporal to reach the level of the parietal notch (the point at which the postparietal processes leave the skull table)

(e) facial process of maxilla set towards rear of bone, premaxillary process horizontally expanded
(f) small number (fewer than 13) of well-spaced maxillary teeth
(g) the obliquity of the vertebral condyles
(h) the waisting of the vertebral condyles
(i) the loss of autotomy septa.

These character states have arisen within Platynota (*sensu* Pregill *et al.* 1986) and, in most cases, their absence in a very early representative would not present great difficulties. Text-figure 16 illustrates currently agreed relationships amongst the Platynota (Borsuk-Bialynicka 1984; Pregill *et al.* 1986) based on derived character states. *Parviraptor* emerges as having a basal position amongst the poorly resolved 'necrosaurs', stem platynotans known from the late Cretaceous to the Oligocene (Estes 1983; Pregill *et al.* 1986). As currently constituted, necrosaurs form a grade rather than a clearly diagnosed monophyletic group, and it is likely that some genera lie closer to the crown than others. Thus the presence of plicidentine in some genera but not others (Estes 1983) is as likely to be due to its primitive absence in some genera as to secondary loss. Some necrosaurs (e.g. *Necrosaurus* from the Palaeocene–Oligocene of Europe; Estes 1983) show a build up of attachment bone around the tooth bases similar to that of *Parviraptor*.

If *Parviraptor* is genuinely platynotan, its presence in the middle Jurassic is not surprising (and was predicted by Borsuk-Bialynicka 1984, p. 67) since the appearance of the possible anguioid *Dorsetisaurus* in the late Jurassic (Portugal, North America) indicates that the primary anguimorph dichotomy had already taken place.

THE ISOLATED ARCHOSAUR TOOTH

The small isolated archosaur tooth on the holotype block (Text-fig. 2, arrowed) has a compressed conical crown and a root which is slightly wider than the crown. Unlike the small crocodilian teeth found at Purbeck, however, the crown does not bear striae. In its general shape, the tooth resembles those of the genus *Lisboasaurus* from the late Jurassic of Portugal (Milner and Evans 1991, fig. 6). Seiffert (1973) described *Lisboasaurus* as an anguimorph, but Estes (1983) noted the resemblance between the type maxilla and that of a small therapod. Milner and Evans (1991) reached the same conclusion, suggesting that the genus might be related to troodonts or, possibly, birds. If the Purbeck tooth is attributable to *Lisboasaurus*, it would provide another link between the Jurassic assemblages of Britain and Portugal.

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